# *Coccidioides* Niches and Habitat Parameters in the Southwestern United States

## A Matter of Scale

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**ABSTRACT: To determine habitat attributes and processes suitable for the growth of *Coccidioides,* soils were collected from sites in Arizona, California, and Utah where *Coccidioides* is known to have been present. Humans or animals or both have been infected by *Coccidioides* at all of the sites. Soil variables considered in the upper 20 cm of the soil profile included pH, electrical conductivity, salinity, selected anions, texture, mineralogy, vegetation types and density, and the overall geomorphologic and ecological settings. Thermometers were buried to determine the temperature range in the upper part of the soil where *Coccidioides* is often found. With the exception of temperature regimes and soil textures, it is striking that none of the other variables or group of variables that might be definitive are indicative of the presence of *Coccidioides*. Vegetation ranges from sparse to relatively thick cover in lower Sonoran deserts, Chaparral-upper Sonoran brush and grasslands, and Mediterranean savannas and forested foothills. No particular grass, shrub, or forb is definitive. Material classified as very fine sand and silt is abundant in all of the *Coccidioides*-bearing soils and may be their most common shared feature. Clays are not abundant (less than 10%). All of the examined soil locations are noteworthy as generally 50% of the individuals who were exposed to the dust or were excavating dirt at the sites were infected. *Coccidioides* has persisted in the soil at a site in Dinosaur National Monument, Utah for 37 years and at a Tucson, Arizona site for 41 years.**

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## INTRODUCTION

*Coccidioides* is a saprophytic fungus occurring in arid and semiarid regions of the New World (Fig. 1). Soils in these areas are the natural reservoir of the organism and are critical for its survival. In the United States it is endemic in parts of Arizona, California, Nevada, New Mexico, Texas, and Utah. It is also endemic in northern Mexico, Central America, and scattered areas in South America. The endemic zones are, with some exceptions, generally arid to semiarid with mild winters, and long hot seasons (Fig. 2). Two species of *Coccidioides* have been described[1]: *Coccidioides immitis*, found in the central valley of California, southern California, and northern Mexico; and *Coccidioides posadasii*, found in the parts of the endemic area outside of California.

Areas where *Coccidioides* is present in soils may be divided into two major types: growth sites and accumulation sites. Growth sites are where physical, chemical, and biological conditions are suitable for completion of the


**FIGURE 1.** *Coccidioides* endemic zones in North, Central, and South America. Endemic areas are shown in gray. Blowup shows endemic areas in the United States, including the 2001 outbreak site in Utah.

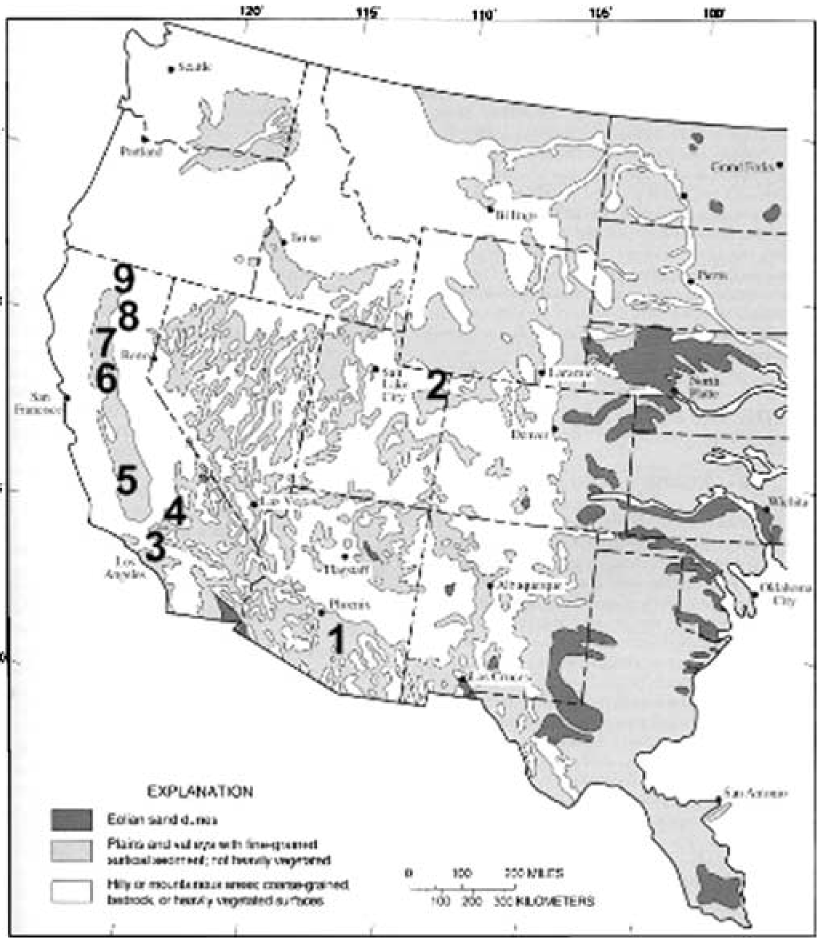


**FIGURE 2.** *Coccidioides* sites sampled by the authors. 1: Tucson, Arizona area, four sites, (3-2B, MEG, MWB, and DP); 2: SS, Swelter Shelter, Dinosaur National Monument, Utah; 3: Santa Susana Mts., near Simi Valley, California, sampled general area, not a specific site; 4: STH, Sharktooth Hill, near Bakersfield, California; 5: WC, White Creek, Diablo Range, western Fresno County, California; 6: CV, Capay Valley, near Brooks, California; 7: WH, Whiskey Hill, 20 miles west of Williams, California; 8: RS, Richardson Springs, near Chico, California; 9: DC, Dye Creek, near Red Bluff, California. Dark gray color = Eolian sand dunes; medium gray color = plains and valleys with fine-grained surficial sediment, not heavily vegetated; light gray = hilly or mountainous areas, coarse-grained sediments, bedrock, or heavily vegetated surfaces. (Map modified from Breed.[2])

entire growth cycle required by the organism. These growth sites are the focus of this study. Accumulation sites are where arthroconidia (spores) of *Coccidioides* may be deposited on or near the soil surface after being transported from growth sites by wind, water, organisms, or anthropogenic means.

Accumulation sites may, under the right circumstances, evolve into growth sites if the necessary environmental conditions are present for growth and if the arthroconidia are protected from adverse environmental or biological conditions. But in many situations the viability of the arthroconidia (especially on or near the soil surface) may be destroyed by exposure to excessive heat, ultraviolet light, or lack of moisture. The time required, *in situ,* for the viability to be lost is unknown, but undoubtedly varies with differing environmental circumstances. It is important to note that soils in both sites may be infectious to animals and humans at any time of the year under the right conditions.

Field and laboratory studies by numerous authors have demonstrated that many physical, chemical, biological, and temporal factors influence the growth of *Coccidioides.*[3–8] Key factors include: amount and timing of rainfall and available moisture, soil humidity, soil temperature, soil texture, alkalinity, salinity, organic content of soils, degree of exposure to sunlight and ultraviolet light, and competition with other microorganisms or plant species or both. Other factors that may be important are the presence of soils derived from marine sedimentary rocks, presence of borates, soil chemistry, presence of Indian middens, and presence of rodent burrows.[7–10]

Trying to identify, rank as to importance, and describe *Coccidioides* soil niches is a daunting task. Soil is one of the most complex natural systems known, involving a wide range of physical, chemical, and biological processes operating and interacting with each other on a vast range of temporal and spatial scales. Soils are continually changing in response to water supply, temperature, organic activity, erosion and deposition, disturbances (both natural and anthropogenic), and time. These changes can take place slowly, over years, decades, or millennia (e.g., continental erosion and deposition, weathering of parent rocks and minerals, and global climate change), or rapidly over months, days, or minutes (e.g., movement of salts and other soluble compounds on account of capillary forces, microbial growth, flooding, and localized erosion due to wind and/or water). Spatially, the endemic zones for *Coccidioides* are measured in hundreds of kilometers, while individual growth sites within endemic areas are measured in meters and centimeters, and niches within the soil profile (defined by physical, chemical, and biological phenomena and associated processes) are measured on scales of millimeters (e.g., soil pore space) or even nanometers (e.g., water films on clays).

## ENDEMIC ZONES

Zones endemic for *Coccidioides* were defined by observations and cataloging the occurrence of coccidioidomycosis in humans and other animals and by skin testing of human populations and cattle.[11–13] Maddy[14] pointed out the concurrence of the areas defined by coccidioidomycosis cases and skin testing with the Lower Sonoran Life Zone (LSLZ) as defined and described by

Merriman.[15] Maddy[14] further suggested (p. 154) that *Coccidioides* can only propagate within the LSLZ. Other researchers have pointed out that there are known *Coccidioides* sites within areas characterized by a Mediterranean climate with different types of flora and fauna from those found in the LSLZ.[7] However, sites examined where *Coccidioides* populations exist in Utah, and in central and northern California, do not share many characteristics with the LSLZ. Most notable is the difference in the types and densities of vegetative ground cover (FIGS. 4–11). In addition, throughout the entire endemic zone, water and temperature are arguably the two main factors, operating at all scales that control and limit the growth and propagation of *Coccidioides*.

## *Water*

Precipitation in the endemic zones of the southwestern United States is characterized by two main regional patterns. The first is a winter rainy season, when most of the annual precipitation occurs that is followed by a prolonged dry season. The second pattern is a rainy winter season followed by a spring dry period and then a second, monsoonal rainy period, during the summer months, which is in turn followed by a drier fall season. The first pattern is characteristic of California, while the second is more typical of Arizona, New Mexico, Texas, and Utah. Annual precipitation within endemic zones generally ranges between 5 cm and 50 cm; however, in northern California near known (FIG. 2) *Coccidioides* sites, annual amounts as great as 66 cm in the Richardson Springs (Mud Creek) area, 63 cm in the Williams (Whiskey Hill) area, and 61 cm in the Red bluff (Dye Creek) area have been recorded (TABLE 1). Rainwater that reaches the ground may evaporate, run off, or infiltrate into the soil. In most cases it will be dispersed by all three methods to varying degrees. More important than the total amount of precipitation is the amount of water that infiltrates the soil profile to depths where *Coccidioides* may exist.

Infiltration of the soil is governed by numerous factors. Topography of the land surface directly affects infiltration as steeper slopes enhance runoff, allowing less time for infiltration, while in flat or depressed areas water will pond or drain off more slowly, allowing more time for infiltration. Infiltration is also affected by the intensity and duration of a precipitation event. Heavy rainfalls of short duration may exceed the infiltration capacity of the soil, resulting in greater runoff than would occur if the same amount of rain fell over a longer period of time. Different types and densities of vegetation can retard runoff, thereby increasing infiltration rates. Plant roots can also enhance infiltration by providing pathways in the soil for water movement. A rough soil surface can slow the runoff and increase the infiltration rate. Infiltration will not occur if the soil is saturated (pore spaces filled with water) prior to a precipitation event.

**TABLE 1. Climate factors (data from the nearest government weather station to each site)**

| | Ambient air temperature (°C) | | | | |
|---|---|---|---|---|---|
| Sites | Average high | Average low | Extreme high | Extreme low | Annual precipitation (cm) |
| 3-2B[1] | 27.7 | 12.7 | 47.2 | 18.8 | 30.5 |
| MEG-s-06[1] | 22.7 | 12.7 | 47.2 | 18.8 | 30.5 |
| MWB-05[1] | 22.7 | 12.7 | 47.2 | 18.8 | 30.5 |
| DP-06[1] | 22.7 | 12.7 | 47.2 | 18.8 | 30.5 |
| SS2-05[2] | 17.7 | –0.5 | 43.3 | –40 | 21.6 |
| SV[3] | 21.1 | 12.7 | 43 | –5 | 30.5 |
| STH-06[4] | 25 | 11.6 | 46.1 | –7.2 | 15.2 |
| WC1-06[5] | 22.2 | 8.3 | 43.3 | –12.2 | 38.1 |
| CV[6] | 23.8 | 8.8 | 44.4 | –6.6 | 57.9 |
| WH[7] | 24.4 | 8 | 46.1 | –6 | 63.5 |
| RS[8] | 23.8 | 8.3 | 47.7 | –12.2 | 66.0 |
| DC[9] | 23.8 | 10 | 48.8 | –7.7 | 60.9 |

[1] Tucson, Arizona.
[2] Dinosaur National Monument, Utah.
[3] Santa Susana Mts., California.
[4] Sharktooth Hill near Bakersfield, California.
[5] White Creek, Diablo Range, western Fresno County, California.
[6] Capay Valley, near Brooks, California.
[7] Whiskey Hill, west of Williams, California.
[8] Richardson Springs, near Chico, California.
[9] Dye Creek, near Red Bluff, California.

Porosity becomes the most important controlling factor as water, driven by gravity, penetrates the soil profile. Soil pores are the open space (voids) between individual soil particles not occupied by solids. Soil pores are always filled with air or water or both in varying proportions. Porosity is determined by the texture, structure, and organic material content of the soil. Permeability is the ability of a soil to transmit water and is also dependent on grain size and shape. Soils with high amounts of same-sized sand particles will have larger continuous pores and will rapidly transmit water and air. In comparison, clay-rich soils, because of the small size of individual particles, will have low permeability and transmit water slowly because of poor connectivity between soil pores and swelling, when wet, of individual clay particles.

Soil texture is the proportion of individual soil particles in different size groups (FIGS. 3, 12). The size most important for microorganisms ranges from clay (<0.002 mm) to sand (0.5 to 2.0 mm). Soil structure is the arrangement of masses of individual soil particles into larger aggregates (sometimes called peds) that are held together by clay minerals, organic material, iron oxides, fungi hyphae, and bacterial polysaccharides.[16] Aggregates are further classified by their size, shape, and cohesion. Between aggregates the pore spaces

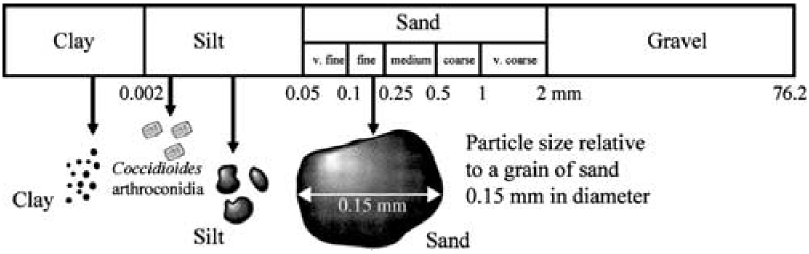


**FIGURE 3.** Size classification of soil particles. Note the relative size of *Coccidioides* arthroconidia compared to sand, silt, and clay particles (U.S. Department of Agriculture).

and their interconnections are larger than the spaces between individual soil particles and, as such, water infiltration is enhanced in well-aggregated soils. When the soil pores are completely filled with water, the soil is said to be saturated and the pore water will eventually drain to lower levels in the profile in response to gravity. Soils that are frequently or continually saturated with water (e.g., swamps, wetlands, and poorly drained areas), that is, areas where the water table is at or very near the surface, are not considered favorable habitats for *Coccidioides*. As water drains from the profile, it is replaced with air. The soil atmosphere in well-aerated soils is similar to air, composed mainly of nitrogen, oxygen, and carbon dioxide. However, respiration by organisms consumes oxygen and releases carbon dioxide; thus in poorly aerated soil, soil

**FIGURE 4.** 3-2B *Coccidioides* site on the alluvial slope of the Santa Catalina Mountains, Tucson, Arizona. Dust from excavation of a ditch infected three humans and three dogs. One dog and one adult human male had severe cases of coccidioidomycosis.

**FIGURE 5.** Landscape adjacent to Swelter Shelter *Coccidioides* site at the edge of an ancient flood plain of the Green River, Dinosaur National Monument, Utah.

with low permeability, and soil within aggregates, carbon dioxide levels are elevated and oxygen levels may fall, even to anaerobic levels.

Available water in the pore spaces, after all of the gravitational water has drained, is held by capillary forces and surface tension between water and solid soil materials. The soil is then described as being at field capacity. Evapotranspiration by plants depletes capillary water and it is also used for nutrient diffusion by microorganisms. As soils dry, water films around soil particles become thinner and bacterial activity and nutrient availability becomes limiting for many microorganisms. Ultimately with continued drying, microorganism activity is confined to filamentous organisms that can use hyphae growth to reach water unavailable to bacteria. It can be speculated that this indeed is a favorable situation for *Coccidioides* to prevail, in drier soils with temperatures too high in the upper soil profiles for robust bacterial activity.

In addition to precipitation, water for *Coccidioides* growth can be supplied by permanent or intermittent streams within, or originating outside of, but flowing through, endemic areas. Numerous *Coccidioides* growth sites are within or on the margins of riparian areas adjacent to these streams. This is the case for the Capay Valley site (FIG. 2, site number 6) within the riparian area along Cache Creek (FIG. 11), Red Bluff (FIG. 2, site number 9) about 100 m from Dye Creek, and Richardson Springs (FIG. 2, site number 8) within 100 m of Mud Creek. It is also reported that sites positive for *Coccidioides* are not uncommonly found next to mostly dry arroyos that carry water only during times of sporadic cloudbursts.[7,8]

**FIGURE 6.** Landscape surrounding Sharktooth Hill *Coccidioides* site near Bakersfield, California. Note the extensive grasslands. The density of ground cover varies with the amount of winter precipitation.

At the Swelter Shelter *Coccidioides* site (FIG. 2, site number 2) in Dinosaur National Monument, Utah annual rainfall is 21 cm. The soils have a very high percentage of fine sandy material with a low water-holding capacity and thus the soils are frequently exceedingly dry. However, directly above the midden area associated with the archeology site is an extensive steeply dipping rock face whereby during rainstorms water runs off the rock face directly onto the Swelter Shelter midden, forming a localized area in the soil favorable for microorganisms including *Coccidioides.*

Swatek[7] suggested that water requirements for *Coccidioides* growth in natural soils can be supplied by relative (soil?) humidities between 56% and 90% for several weeks. Freidman *et al.*[17] pointed out that dry arthroconidia (*Coccidioides* spores) survived for 6 months at temperatures between 15°C and 37°C and at relative humidities (laboratory controlled) greater than 10% and as high as 95%. Also at a humidity of 10% and a temperature of 37°C there was a significant loss of viability. Maddy[14] suggests that elevated soil humidities (humidity of the air within the pore spaces not filled with water) following rainstorms may reach the optimum for *Coccidioides* growth. It is important to point out that because of restrictive connections between soil pore spaces, soil humidities often cannot equilibrate with atmospheric humidities. Under very dry conditions in soils at or even below the wilting point of plants, water is still present as tightly bound films on soil particles and soil aggregates. Thus, the relative humidity within soil pore space is commonly high, often near 100%. In desert environments soil humidities (even near the surface) have been

**FIGURE 7.** White Creek *Coccidioides* site in the Diablo Range, western Fresno County, California. The site is at the base of the large rock outcrop, (upper left corner of photograph); note the dense chaparral and grass understory.

frequently measured above 85%. At the same time the relative humidity of the atmosphere above the soil was at 15%.[18]

### *Temperature*

Temperature, second to water, is the most important factor affecting the physical, chemical, and biological processes within the known endemic zones for *Coccidioides*. Temperature affects microorganisms in many ways, including controlling the rates of respiration, rates of growth for which there are different limiting and optimal temperatures for different organisms, and microbial rhythms, such as dispersal and sporulation. At the microscale, in soil niches, temperature affects oxidation–reduction potentials, pressure, volume, diffusion of soil gases, capillary action, Brownian movement, viscosity, and surface tension.

Soil temperatures are a reflection of the ambient air temperatures and vary accordingly, with a lag time that increases with depth in the soil profile. If the air temperature is greater than the soil temperature, heat will be transferred to the soil. If the soil is warmer than the air, heat will be transferred to the atmosphere above the soil. Large fluctuations in the air temperature result in large fluctuations in soil temperatures. The amplitude of diurnal and seasonal temperature fluctuations decreases with depth in the soil profile. At 50 cm the change in temperatures due to varying surface conditions is not pronounced

**FIGURE 8.** Richardson Springs (Mud Creek) *Coccidioides* site at the extreme southern end of the Cascade Mountains about 8 miles northeast of Chico, California. The site is on a low terrace of Mud Creek; the soils are alluvial material derived from basaltic volcanic sediments, lava flows, breccias, and tuffs, and the climate is Mediterranean.

and at 10 m the soil temperature is nearly constant. Numerous factors affect soil temperature including latitude, altitude, insolation, cloud cover, slope aspect, soil color, organic content, vegetation cover, snow cover, and moisture content. In the endemic zone for *Coccidioides* in the southwestern United States mean annual air temperatures can range from –0.5°C to 24.4°C with extreme lows and highs of –40°C to 48.8°C (TABLE 1). Surface temperatures of soils in the endemic zone range from well below freezing to over 80°C (a temperature lethal for many microorganisms). Spot (isolated individual temperature determinations at selected sites at any given date) temperature readings in our study on July 21, 2006 from a soil in western Fresno County, California near White Creek were taken with an ambient air temperature of 42°C. The soil was dark gray and had a surface temperature of 63°C. At a depth of 2 cm the temperature was considerably less at 35°C, and at a depth of 20 cm the temperature was 30°C. Spot temperatures from a soil at Richardson Springs, California on July 22, 2006 were made with an ambient air temperature of 46°C. Again, the temperature of the dark brown soil at the surface was considerably higher at 70°C. At a 2-cm depth, the temperature had fallen to 40°C, and at 20-cm depth it was 29°C. Comparable measurements in July 2006 at Dye Creek near Red Bluff, California had an ambient air temperature of 47°C. The dark brown soil had a temperature of 82°C at the surface and was 46°C at a 2-cm depth. At 20-cm depth the temperature had dropped to 27°C. These spot temperatures demonstrate that even with high ambient air and higher yet (possible lethal)

**FIGURE 9.** Dye Creek *Coccidioides* site is located 14 miles southeast of Red Bluff, California in the foothills of the Cascade Mountains. Seventeen of 39 participants of an archaeological dig at this site were infected. The soils are a mixture of alluvial and residual material derived from underlying volcanic lava flows, tuffs, and lahars (mudflows). The climate is Mediterranean; note oak and pine trees and the ground cover of yellow star thistle and needle grass.

soil surface temperatures, conditions at a depth of 20 cm are well within the temperature range for optimal growth of *Coccidioides.*

Most, perhaps all, known *Coccidioides* growth sites in Arizona are within soils classified as hyperthermic arid or thermic arid and semiarid (FIG. 13). It is postulated that this is also true for most soils positive for *Coccidioides* throughout the endemic zones outside of Arizona. Hyperthermic soils have an average annual temperature that is greater than 22°C at 50-cm depth. Thermic soils have an average annual temperature between 15°C and 22°C at 50-cm depth. In both instances, if the interface between the soil and the underlying bedrock is less than 50 cm, the temperature is taken at the rock–soil interface. In addition, both hyperthermic and thermic soils have a greater than 5°C difference between the mean annual summer and the mean annual winter temperature measured at 50-cm depth.

*Coccidioides* has frequently been isolated from soils at depths from 2 to 20 cm. A study of soil temperatures that included these depths was made for soil profiles from Arizona, California, and Utah (TABLE 2), which is a statistical summary of the results collected by single self-recording thermometers buried at the indicated depth for about 1 year. Most thermometers were set to record a value every hour; approximately 8,760 individual readings from each thermometer. At three sites (MEG-nw, MEG-s, and MWB) the thermometers

**FIGURE 10.** Landscape adjacent to the Whiskey Hill *Coccidioides* site 20 miles west of the town of Williams, California. The mountainous area is within the California Coast range. The soils are residual material derived from Cretaceous and Jurassic marine sandstone and shale and the climate is Mediterranean.

were set to record a value every 16 min for a year's duration. So for those sites each row of statistical values in TABLE 2 is derived from a population of approximately 32,850 readings from each thermometer. Perhaps, most notable, are the data from the Swelter Shelter site and two nearby locations (most likely negative for *Coccidioides*) in Dinosaur National Monument. Temperatures at these three locations are significantly colder than all of the other sites in Arizona and California at all levels in the soil profiles. Also notable for most sites are the maximum temperatures at the 2-cm depth, which range between 54°C and 60°C with the exception being the OF site in Dinosaur National Monument at 49°C. Temperatures in the high 50s and greater may be lethal for *Coccidioides*, depending on the humidity and duration of exposure.[7,14,17] At the 20-cm depth maximum temperatures were mostly in the 30s and 40s, temperatures possibly close to the optimal for *Coccidioides* growth.

At Dinosaur National Monument three thermometers were placed in soil profiles (2, 10, and 20 cm) at several locations in and near the Swelter Shelter *Coccidioides* site. One profile (SS2-05) was directly within the midden area at the base of a steeply dipping rock outcrop with a shallow overhang, the floor of which was excavated during an archeological dig in 1961. The second profile (OF-05) was located in an open area approximately 100 m east of SS2-05 and away from the bottom edge of the rock face. The third profile (LC-05) was located at the base of the rock outcrop approximately 100 m south of SS2-05. This overall arrangement was designed to test the hypothesis that the southern exposure of SS2-05 and its location at the base of the rock was an

**FIGURE 11.** Capay Valley *Coccidioides* site located near the town of Brooks, California and within the riparian area of Cache creek. Eleven of 23 individuals were infected after excavating this archaeological site. The photograph is looking from the site across Cache Creek. The landscape adjacent to the riparian area is open grasslands with scattered oak trees and the climate is Mediterranean.

environment in which *Coccidioides* could grow; in large part because of the additional moisture washing off the steeply dipping rock face and the warmer soils associated with the southern exposure, lack of shade throughout the entire year, a thin vegetation cover, and heat reflected off the rock face. Temperatures from SS2-05 and LC-05 are somewhat higher than those recorded at OF-05, with median temperatures of 14.2 to 14.8°C versus 11.7 to 12.3° C, respectively. While these temperature differences are not great, they are satisfactory for the growth and propagation of C*occidioides*, as human infections occurred at Swelter Shelter in 1964 during an archeological dig and again 37 years later, in June 2001, during archeological work associated with construction of a wall at the site, and yet again in September 2001, when work was restarted at the site and additional infections occurred.[20,21]

The overall colder temperatures associated with the Swelter Shelter area and in particular the SS2-05 *Coccidioides* site are clearly shown by the median values in FIGURE 14. For Swelter Shelter area samples, 50% of the values lie above the median temperature of 14.9°C, which is within the range considered acceptable for the growth of *Coccidioides*.[8,14] Sites MEG-s and MEG-nw are approximately 200 m apart with similar vegetation density, but MEG-s is on a slightly steeper slope that faces directly south whereas MEG-nw faces northeast. The higher median temperatures at MEG-s versus MEG-nw are the result of the sun aspect and slope gradient on soil temperatures. The overall

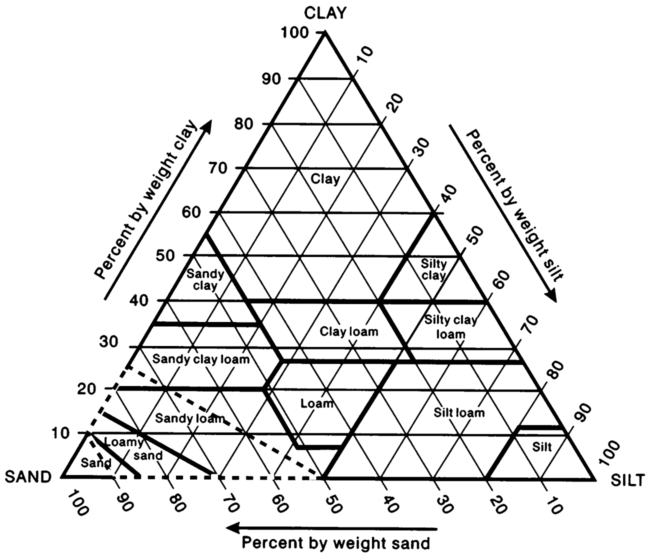


**FIGURE 12.** Textural triangle of sand, silt, and clay. Soils from all *Coccidioides* sites examined to date have textures that lie within the area bounded by the *heavy dashed lines* (U.S. Department of Agriculture).

distributions for all sites are similar at both depths but at the 20-cm depth the maximum temperatures are 10 to 20 degrees colder than the 2-cm maximums. There is less difference between the minimum temperatures at 20 cm, which are mostly 2 to 10 degrees warmer than the 2-cm depth (FIG. 14).

In summary, the growth of *Coccidioides* may be described by six temperature regimes (TABLE 3). The temperature regimes were determined on the basis of laboratory data and field observations and are by no means meant to be definitive. They are at best speculations that require refinement as additional data are obtained. The temperature regimes are: (1) >55° C: lethal in a relatively short time (hours or days, shorter with lower humidities); (2) 40–55° C: somewhat limiting at higher temperatures (especially under drier conditions); (3) 20–40°C: optimal growth temperature range; (4) 5–20°C: growth becoming marginal at lower temperatures in this range; (5) 0–5° C: mostly dormant but arthroconidia still viable; and (6) <0°C: dormant, but viable and capable of growth with increasing temperatures; possibly lethal if exposed to repeated freezing and thawing.

Most remarkable is the large amount of time the soils at both the 2-cm and the 20-cm depths are within temperature regimes favorable for the growth and propagation of *Coccidioides*. Some regional differences are noteworthy. At the 20-cm depth, soils at the Swelter Shelter site are within the 20°C to 40°C range an average of 32% of the year (~ 2,800 h/year). In comparison, the two California sites have soil temperatures in the 20°C to 40°C range

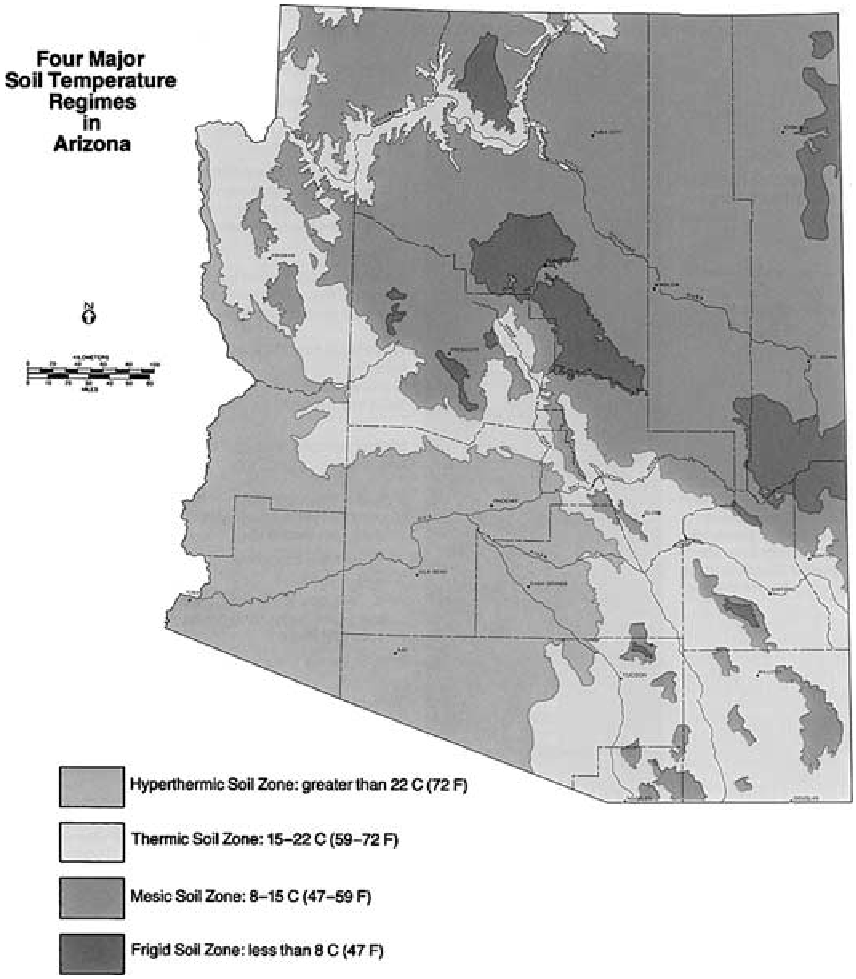


**FIGURE 13.** Soil temperature regimes in Arizona (modified from Hendricks[19]).

an average of 56% of the year (~ 4,900 h/year), and the four Arizona sites with soils in the 20°C to 40°C range, an average of 66% of the year (~ 5,700 h/year). One possible conclusion requiring additional study is that *Coccidioides* may be more prevalent in Arizona soils than California soils. Because of the longer duration of time, Arizona soils are at temperatures most favorable for *coccidioides* growth. If this hypothesis is valid then it may suggest that, all things being equal, Arizona soils may be more infective than soils in California. Also noteworthy is the relatively little amount of time soils at the 2-cm depth are warmer than 55°C. However, soils at White Creek were over 55°C for

**TABLE 2. Soil temperature profiles at *Coccidioides* sites**

| Collection site | Depth (cm) | Soil temperature profile (°C) Maximum | Minimum | Mean | Median | 25 Quartile | 75 Quartile |
|---|---|---|---|---|---|---|---|
| DP- 06[1] | 2 | No data | | | | | |
| DP-06[1] | 10 | 45.3 | 5.4 | 27.4 | 27.9 | 20.9 | 33.2 |
| DP-06[1] | 20 | 40.3 | 6.8 | 26.3 | 27.2 | 20.2 | 31.7 |
| MEG-s-06[1] | 2 | 60.5 | – 0.04 | 25.4 | 24.9 | 15.8 | 33.4 |
| MEG-s-06[1] | 6 | 48.5 | 3.75 | 24.7 | 24.8 | 17.1 | 31.5 |
| MEG-s-06[1] | 12 | 43.5 | 6.9 | 25.3 | 25.4 | 18.2 | 31.8 |
| MEG-s-06[1] | 27 | 39.4 | 13.7 | 26.0 | 26.2 | 19.3 | 32.4 |
| MEG-nw-06[1] | 2 | 54.5 | 0.37 | 22.5 | 22.5 | 13.4 | 29.6 |
| MEG-nw-06[1] | 9 | 48.2 | 3.9 | 23.0 | 22.7 | 14.6 | 30.3 |
| MEG-nw-06[1] | 15 | 41.4 | 7.2 | 23.4 | 23.2 | 15.3 | 30.8 |
| MEG-nw-06[1] | 31 | 38.1 | 12.5 | 24.1 | 23.6 | 16.5 | 30.9 |
| MWB-05[1] | 2 | 54.0 | 1.97 | 24.7 | 24.6 | 15.7 | 32.6 |
| MWB-05[1] | 10 | 43.3 | 7.4 | 24.6 | 24.9 | 15.5 | 32.8 |
| MWB-05[1] | 20 | 40.0 | 9.3 | 24.9 | 25.1 | 15.9 | 32.6 |
| SS2-05[2] | 2 | 57.4 | –3.4 | 16.1 | 14.8 | 5.8 | 24.2 |
| SS2-05[2] | 10 | 43.0 | –1.0 | 15.7 | 14.9 | 5.7 | 24.7 |
| SS2-05[2] | 20 | 35.6 | –0.9 | 14.6 | 14.2 | 5.0 | 23.5 |
| LC-05[2] | 2 | 56.2 | –1.6 | 16.4 | 14.4 | 6.1 | 24.2 |
| LC-05[2] | 10 | 43.8 | –0.52 | 15.4 | 14.3 | 5.6 | 24.0 |
| LC-052 | 20 | 35.7 | 0.69 | 15.1 | 14.3 | 5.9 | 23.9 |
| OF-05[2] | 2 | 49.8 | –6.5 | 14.4 | 12.3 | 3.1 | 22.5 |
| OF-05[2] | 10 | 39.1 | –5.0 | 12.9 | 11.8 | 2.2 | 22.5 |
| OF-05[2] | 20 | 31.7 | –2.9 | 12.1 | 11.7 | 2.4 | 22.4 |
| STH-06[3] | 2 | 55.7 | 2.7 | 24.5 | 22.5 | 14.1 | 33.8 |
| STH-06[3] | 10 | 47.7 | 5.7 | 24.7 | 23.0 | 15.2 | 34.3 |
| STH-06[3] | 20 | 45.8 | 9.8 | 24.5 | 24.1 | 15.9 | 33.3 |
| WC1-06[4] | 2 | 59.8 | 2.7 | 24.1 | 21.8 | 13.0 | 32.6 |
| WC1-06[4] | 10 | 44.3 | 6.3 | 23.2 | 22.5 | 13.8 | 32.1 |
| WC1-06[4] | 20 | 38.7 | 7.4 | 22.0 | 21.8 | 13.2 | 30.0 |

All values measured over a year's duration with individual readings taken mostly at 1-h intervals throughout the year.

[1] Tucson, Arizona.

[2] Dinosaur National Monument, Utah.

[3] Sharktooth Hill near Bakersfield, California.

[4] White Creek, Diablo Range, western Fresno County, California.

1.7% of the year (~ 149 h). Detailed examination of the temperature data from White Creek shows that temperatures greater than 55°C occurred for five continuous hours on 14 days, for four continuous hours on 9 days, and for three continuous hours on 12 days during July and August of 2005 and July of 2006.

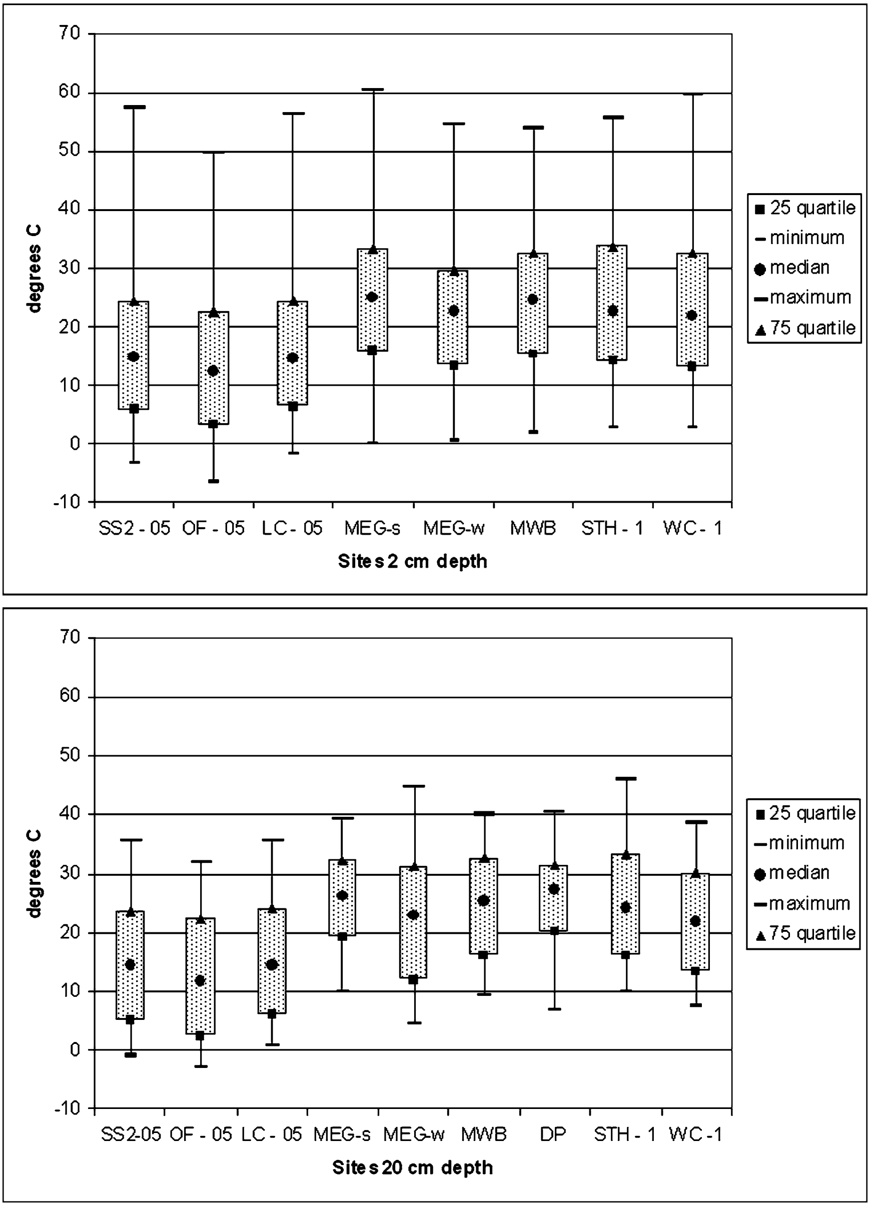


**FIGURE 14.** Box plots of soil temperatures at *Coccidioides* sites. Utah (SS2-05, OF-05, LC-05), Arizona (MEG-s, MEG-w, MWB, DP), and California (STH-1, WC-1). Data are not available for the 2-cm depth at the DP site. These box plots use TABLE 2 data and give the data maximum and minimum values, the median as the measure of central tendency, and the box containing the middle 50% of the data delineated by the 25th and 75th quartiles.

## *Texture*

As previously mentioned texture is the relative proportions of sand, silt, and clay in a given soil (FIGS. 3, 12). Soils from all of the *Coccidioides* sites examined in this study so far fall within the domain shown by the heavy dashed line on FIGURE 12. These soils are best described as loamy sand or sandy loams. In general, soils with a high amount of sand-sized material have relatively low water-holding capacity, are more susceptible to wind erosion, and most often are poorly aggregated. Mineralogically, sand-sized material in most soils is composed primarily of quartz with much smaller (1 or 2%) amounts of other silicate minerals (e.g., feldspar, pyroxene, hornblende, and mica). Quartz ($SiO_2$) is chemically quite inert, and as such, its predominance in sandy soils may make it somewhat less favorable for robust permanent microbial colonies, given its poor nutritional status.

Silt-sized material is, in most cases, still dominated by the mineral quartz. The much smaller overall size of the individual silt particles (FIG. 3) and consequently greater surface areas and larger volume of pore spaces give silt a greater water-holding capacity than sand. Silts generally have a lower permeability than sand because the connections between pore spaces in silt are narrower and more restrictive to the movement of water. Because of the greater surface areas in silts, silicate minerals (other than quartz) will chemically degrade faster, providing nutrients for utilization by microorganisms.

The clay-sized fraction of soils is unquestionably of great importance to all soil microorganisms. Some of the clay-sized material in soils is composed of primary rock-forming minerals (quartz, feldspar, and mica). However, most of the clay-sized particles are composed of secondary minerals formed from the weathering and chemical breakdown of the primary minerals. These secondary clay-sized minerals are the most important determinants of the chemical characteristics of most soils. Clay minerals are hydrous aluminum phyllosilicates with mineralogical structures built from layers of $SiO_4$ tetrahedral bound to layers of (Al, Mg, Fe)(O,OH) octahedral cations. Cations of potassium, sodium, and calcium may also often be bound to the negatively charged clay particles. Clays have a much greater surface area, higher cation exchange capacity, and greater water-holding capacity than sand or silt. Clays are chemically active and their negative charge allows for considerable interaction with organic materials and microorganisms (TABLE 2).[22] The ionic charges on clays provide for the slow release of nutrients to the pore environment. Clays may adhere to the surface of larger silt and sand particles, thereby providing additional areas for microbial colonization.

The distribution of fine-grained surficial sediments in the western United States is shown in FIGURE 2. Comparison of FIGURE 1 with FIGURE 2 shows a close correspondence between the areas mapped as endemic for *Coccidioides* and the distribution of fine-grained material in the southwestern United States. Texture analysis of soils from all of the *Coccidioides* sites examined in this

**TABLE 3. Percentage time on an annual basis that soil temperatures were within ranges favorable or unfavorable for the growth of *Coccidioides***

| | | | | Percentage time in each temperature range | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Sites[1] | Collection dates | Reading frequency | Total hours | <0° | 0–5° | 5–20° | 20–40° | 40–55° | >55° |
| 2-cm depth | | | | | | | | | |
| MEG-s[2] | 3/18/05-3/14/06 | 16 min | 8,672 | 0.003 | 2.1 | 32.9 | 51.1 | 12.9 | 0.8 |
| MEG-nw[2] | 3/18/05-3/14/06 | 16 min | 8,672 | 0 | 3.3 | 39.5 | 48.8 | 8.2 | 0 |
| MWB[2] (5 cm) | 2/4/05-1/29/06 | 16 min | 8,663 | 0 | 1.3 | 37.7 | 49.0 | 11.6 | 0 |
| DP-06[2] | no data | – | – | – | – | – | – | – | – |
| SS2-05[3] | 6/20/04-6/20/05 | 1 h | 8,753 | 5.0 | 16.7 | 41.2 | 32.5 | 4.0 | 0.1 |
| OF-05[3] | 6/20/04-6/20/05 | 1 h | 8,753 | 2.8 | 26.0 | 38.9 | 28.5 | 3.2 | 0 |
| LC-05[3] | 6/20/04-6/20/05 | 1 h | 8,752 | 1.1 | 19.5 | 42.9 | 31.3 | 4.6 | 0.07 |
| STH-1[4] | 7/08/05-7/20/06 | 1 h | 9,001 | 0 | 0.9 | 42.6 | 42.6 | 13.7 | 0.07 |
| WC-1[5] | 7/10/05-7/21/06 | 1 h | 9,034 | 0 | 1.1 | 44.9 | 41.1 | 11.8 | 1.7 |
| 20-cm depth | | | | | | | | | |
| MEG-s[2] | 3/18/05-3/14/06 | 16 min | 8,672 | 0 | 0 | 29.6 | 70.3 | 0 | 0 |
| MEG-nw[2] (15cm) | 3/18/05-3/14/06 | 16 min | 8,672 | 0 | 0 | 39.9 | 59.0 | 1.0 | 0 |
| MWB[2] (17cm) | 2/4/05-1/29/06 | 16 min | 8,662 | 0 | 0 | 34.7 | 64.7 | 0.17 | 0 |
| DP-06[2] | 2/16/06-11/17/06 | 1 h | 6,577 | 0 | 0 | 25.4 | 74.3 | <1 | 0 |
| SS2-05[3] | 6/20/04-6/20/05 | 1 h | 8,753 | 0.8 | 23.1 | 43.3 | 32.4 | 0 | 0 |
| OF-05[3] | 6/20/04-6/20/05 | 1 h | 8,753 | 17.0 | 16.0 | 37.0 | 29.5 | 0 | 0 |
| LC-05[3] | 6/20/04-6/20/05 | 1 h | 8,752 | 0 | 20.8 | 45.3 | 33.6 | 0 | 0 |
| STH-1[4] | 7/08/05-7/20/06 | 1 h | 9,001 | 0 | 0 | 40.9 | 58.9 | 0 | 0 |
| WC-1[5] | 7/10/05-7/21/06 | 1 h | 9,034 | 0 | 0 | 45.2 | 54.7 | 0 | 0 |

[1] Unless noted, thermometers were placed at either 2- or 20-cm depths.
[2] Tucson, Arizona.
[3] Dinosaur National Monument, Utah.
[4] Sharktooth Hill near Bakersfield, California.
[5] White Creek, Diablo Range, western Fresno County, California.

study was done by dry-sieving samples of all soil material less than 2 mm in size. The total percentage of soil material between 0.05 mm and 0.25 mm in size at different *Coccidioides* sites is shown in TABLE 4. This very fine-to-fine sand-sized soil fraction is notably present at all sites visited during this study and may be a characteristic common to all *Coccidioides* sites in the southwestern United States. In some sites (SS2-05, STH-06, WC1-06, DP) this very fine sandy material, comprising mostly quartz ($SiO_2$), makes up the major proportion of the soil. All of these sites were associated with notably high rates of infection (often >70%).

### *Chemical Characteristics*

The role of oxygen, carbon, and nitrogen was not assessed in this study, but these elements are all necessary for the growth of *Coccidioides*. Furthermore, these elements must be available in an environment that provides a physical and chemical setting whereby *Coccidioides* can complete its specific biological functions required for life. At the centimeter scale, in the upper parts of sandy well-aerated soils common to the endemic areas of the southwestern United States, the availability of oxygen is unlikely to be limiting to the growth of *Coccidioides*. However, deeper within the soil profile (at a millimeter or smaller scale), if the permeability is low, anaerobic conditions may exist and become a limiting factor.

Carbon and nitrogen required for fungal growth are derived from organic material contained in the soils. The distribution of organic material (controlled largely by vegetation) within the endemic areas of the southwestern United States ranges from sparse in desert areas to abundant in Mediterranean savannas and forested foothills. Visual estimates of organic material in soil samples collected in this study suggest that soils from the deserts of Arizona contain significantly less organic material than the soils collected from California.

One goal of this study was to search for characteristics that might be common to all of the soils from the 13 different known *Coccidioides* sites. The variables investigated are summarized in TABLE 4 and included pH, electrical conductivity, and concentration of fluoride, nitrates, and sulfate. A paste derived from a one-to-one extract with distilled water was used to determine the pH. Arizona soils are slightly more basic and have a smaller range in values than soils from the California sites. The overall range in pH from 6.1 to 8 suggests that, in the natural environment, pH is not a limiting factor for the growth of *Coccidioides* (at least in mid range values). Salinity, derived from the electrical conductivity, is high in three sites and relatively low in all the rest. High sulfate values at Swelter Shelter, Sharktooth Hill, and soils from near Simi Valley (Santa Susana Mts.) are due to the presence of gypsum (calcium sulfate), which was not identified at any of the other sites. The high nitrate

**TABLE 4. Physical and chemical parameters of *Coccidioides* sites**

| Sites | % fines[1] | pH 1:1 extract | Elect. conduct.[2] (μS/cm) | Salinity (mg/L) | Fluoride (μg/g) | Chloride (μg/g) | Nitrate (μg/g) | Sulfate (μg/g) |
|---|---|---|---|---|---|---|---|---|
| 32B[3] | 36 | 7.76 | 490 | 247 | <2.0 | 4.23 | 68.6 | 16.7 |
| MEG-s[3] | 35 | 7.96 | 631 | 332 | <2.0 | 9.90 | 97.5 | 44.9 |
| MEG-nw[3] | 28 | 7.86 | 349 | 176 | no data | no data | no data | no data |
| MWB-05[3] | 25 | 7.61 | 448 | 225 | no data | no data | no data | no data |
| DP[3] | 58 | 8.02 | 300 | 153 | <2.0 | 9.68 | 61.8 | 19.1 |
| SS2-05[4] | 83 | 7.38 | 3200 | 1600 | 3.91 | 169 | 993 | 2870 |
| SV[5] | 46 | 7.36 | 3900 | 1370 | 2.12 | 19.5 | 63.5 | 13,000 |
| STH-06[6] | 69 | 6.15 | 3700 | 1910 | 7.5 | 32.2 | 91.6 | 15,000 |
| WC1-06[7] | 72 | 7.86 | 343 | 174 | <2.0 | 3.82 | <10.0 | 9.71 |
| CV[8] | 19 | 7.46 | 301 | 151 | 3.31 | 10.6 | 12.7 | <15.0 |
| WH[9] | 40 | 7.81 | 430 | 216 | <2.0 | 8.18 | <10.0 | 15.1 |
| RS[10] | 32 | 6.82 | 251 | 126 | no data | no data | no data | no data |
| DC1[11] | 20 | 6.8 | 3 83 | 191 | <2.0 | 13.3 | 51.0 | 23.7 |

[1] Percentage of soil material between 0.05 mm and 0.25 mm in size.
[2] Electrical conductivity.
[3] Tucson, Arizona.
[4] Dinosaur National Monument, Utah.
[5] Santa Susana Mts., California
[6] Sharktooth Hill near Bakersfield, California.
[7] White Creek, Diablo Range, western Fresno County, California.
[8] Capay Valley, near Brooks, California.
[9] Whiskey Hill, west of Williams, California.
[10] Richardson Springs, near Chico, California.
[11] Dye Creek, near Red Bluff, California.

value from the Swelter Shelter soils is probably due to the frequent utilization of the area by birds. Fluoride and chloride are not notable at any of the sites. No one chemical parameter or group of parameters addressed in this study displays a consistent pattern throughout all the sites. This conclusion is in concurrence with the observations of Swatek[6,7] from his studies of midden sites and adjacent soils in California.

Several factors not considered in this study have been suggested as influencing the growth of *Coccidioides*. Elconin *et al.*[23] showed in an 8-year study that high levels of salinity in surface soils could be correlated with the growth of *Coccidioides.* Egeberg *et al.*[5] demonstrated that high soil temperatures and salinity suppressed the growth of bacterial antagonists while enhancing the growth of *Coccidioides.* Pappagianis[8] and Egeberg[10] noted that anomalously high amounts of boron were associated with soils positive for *Coccidioides.* However, these and other factors are not universally observed (this article and Swatek[7]) at all sites known to be positive. One conclusion is that these and other associations are not necessary for the growth of *Coccidioides*, but instead their presence in a given soil may enhance that site by creating an environment more favorable for *Coccidioides*. The improved favorability may be due to any number of reasons; for example, higher organic content may increase the available nutrients, high salinities may reduce competition from other microorganisms, high temperatures may also reduce bacterial numbers, thereby also reducing competition, and high concentrations of sodium borate may be antiseptic for some soil microorganisms but not for *Coccidioides*.

## DISCUSSION

During the 20th century *in situ* field studies of the habitat of *Coccidioides* began with the first separation[24] of the organism from the soil in 1932 and reached a peak[25] during the 1950s through the 1970s. With the advent of major advances in the medical field, attention shifted from the soil habitat to the dimorphic parasitic habitat in the lung and the development of new therapies, medicines, and the search for vaccines. While isolated outbreaks were investigated in the last decades of the century, *in situ* field studies waned. However, in the late 1990s and early in the 21st century, investigations[26–29] of soils using polymerase chain reaction (PCR) techniques that allow microbial detection and isolation of DNA directly from soils opened a new era of interest in the soil habitat. In 2001 the outbreak of coccidioidomycosis in Dinosaur National Monument sparked new studies by multidisciplinary teams of earth scientists, microbiologists, and medical doctors of the soil habitat there and at other sites in Arizona and California.[20,21]

Major technological advances in the last two decades provide powerful tools for examining the soil environments favorable for the growth of *Coccidioides*. Examples are PCR techniques as mentioned above; microelectronics that enable physical properties to be determined at the micrometer scale; more powerful computers capable of simulating and modeling complex natural systems; biosensors that are sensitive to a wide range of chemical compounds; and the discoveries of the properties and behavior of nanometer-sized soil particles. Research opportunities abound in the study of the ecology of the saprophytic habitat of *Coccidioides*. These opportunities are best undertaken by a multidisciplinary approach, with the knowledge of the vast spatial and temporal scales involved, and an understanding that soil is a complex system characterized by the interaction of numerous physical, biological, and chemical processes with diverse parameters. These interactions are most typically nonlinear, nonreversible, and difficult to quantify. In such systems the behavior of the system as a whole cannot be predicted by the behavior of its individual agents or processes. New methods needed to help with future research on *Coccidioides* include development of standardized PCR techniques capable of detecting *Coccidioides* routinely from minimally processed soil samples and development of noninvasive *in situ* techniques to characterize the utilization of pore space by *Coccidioides* in the soil profile. Also needed are fractal models of soil structures found in sites positive for *Coccidioides*. Important questions yet to be answered include the discovery of the microbial antagonists of *Coccidioides* and whether there are temporal cycles of competition with *Coccidioides*. Other questions are: What *in situ* substrates are used by *Coccidioides* and what is the activity (growth/death/dormancy) of *Coccidioides* in response to nutrient fluxes in the vadose zone? Also are these nutrient fluxes affected by clay mineralogy and abundance? And most importantly we need a description of the life cycle of *Coccidioides* in the soil from the initiation of mycelium growth to the development of arthroconidia to dormancy, as well as the knowledge that the role that physical, chemical, and biological processes play in the different chases of the cycle. Answering these and other detailed questions would bring us closer to a more complete understanding of the integral life cycle of this organism and help us predict how the infectious areas might change with global shifts in climate and resulting patterns of desertification.

## REFERENCES

1. FISHER, M.C., G.L. KOENIG, T.J. WHITE, *et al*. 2002. Molecular and phenotypic description of *Coccidioides posadasii* sp. nov., previously recognized as the non-California population of *Coccidioides immitis*. Mycologia **94:** 73–84.
2. BREED, C.S.1999. Monitoring surface changes in desert areas. *In* Desert Winds, Monitoring Wind-Related Surface Processes in Arizona, New Mexico, and California. C.S. Breed & M.C. Reheis, Eds.:1–27. U.S. Geol. Survey Prof. Paper 1598.
3. FIESE, M.J. 1958. Coccidioidomycosis. Charles C Thomas. Springfield, IL.
4. SORENSEN, R.H. 1964. Survival characteristics of mycelia and spherules of *Coccidioides immitis* in a simulated natural environment. Am. J. HYG. **80:** 275–285.

5. EGEBERG, R.O., A.E. ELCONIN & M.C. EGEBERG. 1964. Effect of salinity and temperature on *Coccidioides immitis* and three antagonistic soil saprophytes. J. Bact. **88:** 473–476.
6. LACY, G.H. & F.E. SWATEK. 1974. Soil ecology of *Coccidioides immitis* at Amerindian middens in California. Appl. Microbiol. **27:** 379–388.
7. SWATEK, F.E. 1975. The epidemiology of coccidioidomycosis. *In* The Epidemiology of Human Mycotic Diseases. Y. Al-Doory, Ed.: 75–102. Charles C Thomas. Springfield, IL.
8. PAPPAGIANIS, D. 1988. Epidemiology of coccidioidomycosis. Curr. Top. Med. Mycol. **2:** 199–238.
9. MADDY, K.T. 1957. Ecological factors of the geographic distribution of *Coccidioides immitis*. J. Am. Vet. Med. Assoc. **130:** 475–476.
10. EGEBERG, R.O. 1962. Factors influencing the distribution of *Coccidioides immitis* in soil. *In* Recent Progress in Microbiology, 8th meeting.: 652–655.
11. SMITH, C.E. 1951. Diagnosis of pulmonary coccidioidal infections. Calif. Med. **75:** 385–391.
12. MADDY, K.T., H.G. CRECELIUS & R.G. CORNELL. 1961. Where can coccidioidomycosis be acquired in Arizona. Ariz. Med. **18:** 184–194.
13. PAPPAGIANIS, D. 1980. Epidemiology of coccidioidomycosis. *In* Coccidioidomycosis. D.A. Stevens, Ed.: 63–85. Plenum Medical Book Company. New York.
14. MADDY, K.T. 1957. Ecological factors possibly relating to the geographic distribution of *Coccidioides immitis*. Proceedings of the Symposium on Coccidioidomycosis.U.S. Public Health Service, Pub. No. **575:** 144–157. CDC, Atlanta, GA.
15. MERRIAM, C.H. 1898. Life zones and crop zones of the United States. Div. Biol. Survey Bull. **10:** USDA, Washington, DC.
16. SINGER, M.J. 1991. Physical properties of arid region soils. *In* Semi-Arid Lands and Deserts. J. Skujins, Ed.: 81-109. Marcel Dekker. New York, NY.
17. BERMAN, R.J., L. FREIDMAN, D. PAPPAGIANIS, *et al*. 1956. Survival of *Coccidioides immitis* under controlled conditions of temperatures and humidity. Am. J. Pub. Health **46:** 1317–1324.
18. CAMERON, R.E. 1966. Properties of desert soils. *In* Biology and the Exploration of Mars. C.S. Pittendrigh, W. Vishniac, J.P.T. Pearman, Eds. National Academy of Sciences–Natural Research Council, NASA. Washington, DC.
19. HENDRICKS, D.M. 1985. Arizona Soils. College of Agriculture Centennial Publication, The University of Arizona, Tucson, Arizona.
20. FISHER, F.S., M.W. BULTMAN, D. PAPPAGIANIS, *et al*. 2002. The ecology of the Swelter Shelter *C. immitis* site, Dinosaur Nat. Monument, UT. *In* Proceedings of the Annual Coccidioidomycosis Study Group Meeting, Meeting number **46:** 3. J. Galgiani, Ed. The Valley Fever Center for Excellence, Tucson, AZ.
21. PETERSEN, L.R., S.L. MARSHAL, C. BARTON-DICKSON, *et al*. 2004. Coccidioidomycosis among workers at an archeological site, northeastern Utah. Emerg. Infect. Dis. **10:** 637–642.
22. CHENU, C. & G. STOTZKY. 2002. Interaction between microorganism and soil particles: an overview. *In* Interactions Between Microorganisms and Soil Particles. P.M. Huang, J.M. Bollag & N. Senesi, Eds.: 3–40. John Wiley & Sons. Hoboken, NJ.
23. ELCONIN, A.E., R.O. EGEBERG & M.C. EGEBERG. 1964. Significance of soil salinity on the ecology of *Coccidioides immitis*. J. Bact. **87:** 500–503.
24. STEWART, R.A. & K.F. MEYER. 1932. Isolation of *Coccidioides immitis* (Stiles) from the soil. Proc. Soc. Exp. Biol. Med. **29:** 937–938.

25. STEVENS, D.A. 1980. Coccidioidomycosis. Plenum Medical Book Company. New York, NY.
26. BURT, A., B.M. DECHAIRO, G.L. KOENIG, *et al*. 1997. Molecular marker reveals differentiation among isolates of *Coccidioides immitis* from California, Arizona, and Texas. Mol. Ecol. **6:** S781–S786.
27. DANIELS, J.I., W.J. WILSON, T.Z., *et al*. 2002. Development of a quantitative Taqman-PCR assay and feasibility of atmospheric collection for *Coccidioides immitis* for ecological studies: final report. UCRL-ID-146977. Lawrence Livermore National Laboratory, Livermore, CA.
28. FISHER, M.C., T.J. WHITE & J.W. TAYLOR.1999. Primers for genotyping single nucleotide polymophisms and microsatellites in the pathogenic fungus *Coccidioides immitis*. Mol. Ecol. **8:** 1075–1092.
29. GREENE, D.R., G.L. KOENIG, M.C. FISHER, *et al*. 2000. Soil isolation and molecular identification of *Coccidioides immitis*. Mycologia **92:** 406–410.